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Comment

Comment on Functional landscape connectivity for a select few: Linkages do not consistently predict wildlife movement or occupancy. Autumn R. Iverson, David Waetjen, Fraser Shilling

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ABSTRACT

Ecological connectivity is increasingly acknowledged as crucial for biodiversity conservation. Iverson et al. suggest that increasing stewardship to ensure permeability is a better approach than protecting linkages between protected areas. We argue that the optimal approach depends on the landscape context, conservation goals, and species involved and suggest that linkage plans can prioritize specific places for protection and improved management. However, when using connectivity models as predictive tools, model validation is vital. We commend Iverson et al. for assessing whether modeled linkages were important predictors of species presence. We disagree, though, with the authors' conclusion that their findings challenge the theory and practice of modeling linkages and explain that the reason may be the misalignment of the validation assumptions with model objectives. We offer our perspective on best practices for conducting validation studies and note factors to consider with respect to data used for model validation and model expectations.

Connectivity models characterize the degree to which the landscape facilitates or impedes movement. Linkage models, a specific type of connectivity model, identify where organisms are most likely to move across the landscape, or to move with least cost to their fitness (e.g., in energy use or risk), generally between areas of "resident" or "core" habitat that can support breeding populations (e.g., Beier et al., 2008; Ghoddousi et al., 2021; Wasserman et al., 2013). Establishing ecological networks for conservation that consist of protected and conserved areas connected by linkages (aka ecological corridors; Hilty et al., 2020) is a key conservation tool in landscapes with high levels of human impact or development pressures. Conserving connectivity, including protecting and restoring migration corridors and linkages, is increasingly recognized as a critical component of conservation planning, as shown by an influx of both global initiatives and habitat connectivity legislation passed across the US during the past five years (Hilty and Laur, 2021, Sito and Christian, 2024).

Iverson et al. (2024) suggest that increasing stewardship to ensure permeability is a better approach than protecting linkages between protected areas. As researchers or practitioners involved in the work reviewed and discussed by Iverson et al., as well as other similar modeling projects, we believe that the best approach depends on landscape context, conservation objective, and species of interest (Belote

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et al., 2020; Cameron et al., 2022). Discounting the importance of linkage plans could have grave consequences for connectivity conservation. This is particularly relevant if or when project planners mistakenly question the validity of linkage plans based on a single study.

Connectivity is required at multiple scales, for regular daily movements to find food or cover, and for less frequent but very important long-distance movements including dispersal and migration. Linkages protected through land ownership or easements, and those that align with wildlife-crossing infrastructure across roads are essential for effective connectivity conservation, to ensure the long-term conservation of contiguous, intact movement pathways between core habitat areas. Linkage plans help prioritize specific places for protection, improved management, wildlife crossings, and additional monitoring. Maps developed from connectivity models are also used for prioritizing funding for alternative interventions intended to increase landscape permeability, like making livestock fences more wildlife-friendly, removing barrier fencing (e.g., Linden et al., 2023; McInturff et al., 2020), or prioritizing 'amphibian crossing brigade' effort locations (Kirk et al., 2014).

If connectivity models are used as predictive tools, it is important to test their assumptions and predictions. We applaud Iverson et al. for their work to assess whether modeled linkages identified in several state-wide and regional connectivity planning efforts in California "were important predictors of species presence on the landscape." Iverson et al. state in the discussion that 'linkage models' performed well and "could be effective conservation tools" when tied to measures of human disturbance for migratory or human-sensitive species and when connectivity models included information for focal species. We agree. Yet the authors conclude that their results bring "into question the theory and approach of modeling hypothetical linkages for general species connectivity and the practice of using the resulting maps to inform transportation mitigation, land conservation, and development decisions" (p. 9,10). We do not think this conclusion is warranted based on the data and results presented. Rather, their results support the idea that linkage models work well for species sensitive to human modifications.

Iverson et al. base their conclusion regarding the relevance of linkage models for conservation planning on an analysis in part by using data from human-tolerant species to assess models that were built to predict where human-sensitive species will move. When their assumptions align with the objectives of the models – testing the connectivity model with human-sensitive species (black bears, mountain lions, bobcats) – their results validate the connectivity models. The 'linkage models' predicted roadkill patterns for human-sensitive species, including black bear and mountain lion, which were positively associated with all four California-wide models (Iverson et al., Fig. 3). Similarly, almost all of the best-performing occupancy models included the linkages. The goal of structural connectivity models is to capture coarse-filter connectivity needs to enhance conservation of species. Thus, Iverson et al. provide evidence in support of the use of connectivity models for conservation planning. In addition, the validation results of the one model that included species-specific considerations (DRECP-Penrod) showed that the model worked well for the focal species (desert tortoise *Gopherus agassizii*) and a rare snake species (*Arizona elegans*). While connectivity models may not always work as intended (Iverson et al. cite LaPoint et al., 2013 as an example), several papers have validated linkage models (e.g., Phillips et al., 2021; Puyravaud et al., 2017; Santos et al., 2013; Torretta et al., 2021).

1. Aligning model validation assumptions with model objectives

When validating linkages, the scale of species and landscape data used for validation needs to match the model objectives (Fletcher et al., 2013, 2016). The framing of the Iverson et al. paper implies that the five 'linkage models' included in the validation have the same purpose, but in fact they have different purposes, methods, spatial scales, and assumptions. While Iverson et al. refer to them as 'linkage models', here we refer to them as 'connectivity models' instead, because only two of the five studies are 'linkage' models. Iverson et al. transformed the outputs from three of the connectivity models in order to assess all five models as binary representations of linkages and 'wilderness areas' and assess them at a common extent and resolution. As the authors of the referenced connectivity datasets, we address potential errors introduced by Iverson et al.'s model transformation and mismatch of spatial scale and note additional considerations when assessing or using these models for conservation planning.

The California Essential Habitat Connectivity Project (CEHC; Spencer et al., 2010) and The Nature Conservancy (TNC)-Omniscape maps (Schloss et al., 2021) are based on species-agnostic landscape connectivity models; neither was based on analyses of species-specific habitat or movement needs. While the CEHC classifies the landscape into discrete cores (natural landscape blocks) and linkages, the TNC-Omniscape model is a gradient-based approach that characterizes the entire landscape along a spectrum of connectivity potential. The TNC Omniscape model does not rely on an a priori definition of core habitat areas; thus, it was not designed to be classified into 'linkages' and 'wilderness areas'. In addition, the resolution of the TNC-Omniscape model is much finer (90 m grid cells) than that of the Iverson et al. validation analysis (1 km or 10 km grid cells), causing the importance of narrow linkages to potentially be lost when using the percent of linkage within a larger grid cell as a predictive variable. The Linkage Network for the California Deserts (Desert Renewable Energy Conservation Plan (DRECP)-Penrod: Penrod et al., 2012) is a linkage design that incorporates species-specific habitat and movement needs into a linkage prioritization; therefore, it is a better candidate for validation with focal species data. The Areas of Conservation Emphasis (ACE; California Department of Fish and Wildlife 2019) and the layer by Nuñez et al. (in prep.) are aggregations of several existing connectivity models (including the CEHC, TNC-Omniscape, and DRECP-Penrod layers assessed by Iverson et al.). ACE aggregates data into 2.5-mi^2 hexagons and ranks the hexagons by connectivity conservation importance based on factors including whether a linkage intersects the hexagon; but it does not integrate species richness data as described in the paper. Rescaling ACE hexagon data to a smaller grid cell size likely introduces significant error.

2. Best practices for model validation studies

Because we agree with Iverson et al. that validating connectivity models is important and hope to see model validation applied more frequently, we offer our perspective on best practices for conducting validation studies.

(1) Only single models, or multiple models with the same connectivity objectives, should be subject to validation because the validation metric must be tied to the original study objective. While testing how wildlife-vehicle collision rates or other metrics correlate with ensemble models can be interesting – for example, "do areas that score highly across many connectivity models and objectives also have high wildlife-vehicle collision rates?" – this type of analysis is not a model validation study.
(2) Validation data sets need to match the objectives of the connectivity model. Common objectives of structural connectivity models are to promote movements of large, mobile mammals that are sensitive to human modification, or to facilitate range shifts of species with short dispersal distances in response to climate change (e.g., Schloss et al., 2021). We recommend validating these models using observation of species that are not tolerant of human modification.
(3) Data used to model connectivity should be independent from the data used to validate the outputs.
(4) Data on wildlife movement from camera traps, snow-tracking, telemetry, and genetic analyses can be used in properly

designed local-scale studies to test whether wildlife move more through modeled linkages than adjacent areas of non-linkage habitat. Importantly, the resolution at which validation data were collected needs to match the resolution of the linkage models.

(5) When using wildlife-vehicle collision data for validation, accounting for factors such as traffic volume, human observation biases, species natural histories, and the terrain is important.

(6) Linkages may have different objectives in shared landscapes than heavily modified landscapes (Locke et al., 2019). Stratifying the study area is a recommended approach to evaluate whether linkage models do a better job in differently impacted landscapes (Belote et al., 2020).

3. Additional considerations in connectivity model validation

We also note some factors with respect to data used for model validation and model expectations that should be considered.

(1) Using wildlife-vehicle collisions as a proxy for wildlife movement in linkages assumes that collision risk is heightened where linkages bisect roads. However, highways with high traffic volume may be avoided by many species (Beringer et al., 1990; Gagnon et al., 2007; Riley et al., 2006). Roadkill numbers will be low in these areas as a result, although linkage models may suggest this is where road-crossing structures could be most beneficial. Additionally, several studies indicate that movement linkages and high road mortality sites are not spatially associated and are characterized by different environmental attributes (Cerqueira et al., 2021; Findo et al., 2019; Neumann et al., 2012).

(2) Bias in wildlife-vehicle collision data must be considered. Vehicle accident data, such as that recorded by the California Highway Patrol, are biased towards higher traffic areas and large-bodied animals that require reporting of collisions for insurance purposes (Huijser & Begley, 2019). Roadkill observation data, such as that in the California Roadkill Observation System database, may vary in observer effort by region and road type, especially if based on volunteer-collected observations. Therefore, the absence of wildlife-vehicle collision data does not necessarily equal the non-occurrence of collisions, or a lack of crossing by animals. Variation in the datasets may also be explained by geographic variations in species' abundances and avoidance behaviors, including responses to high traffic volume (Zimmermann Teixeira et al., 2017). These potential biases and the possibility of animal avoidance warrant significant circumspection when drawing conclusions.

(3) Inference of non-detections should be done with caution. While inferring non-detections of a selected species based on detections of a similar or related species can be a valid approach (e.g., Kery et al., 2010), this method requires appropriate survey methods and similar detection probabilities (e.g., bird counts where all species are counted). Species in the class Mammalia can have very different geographic ranges or habitat requirements, as well as disparate detection probabilities, which should be considered when inferring non-detections. Datasets which only track a subset of species, such as the California Natural Diversity Database (CNDDB), should never be used to infer non-detections of non-tracked species (see CNDDB Data Use Guidelines at https://wildlife.ca.gov/Data/CNDDB).

(4) Occupancy rates within linkages may be low for wide-ranging species with large area requirements. Linkage plans are aspirational in that they strive to maintain or improve connectivity (e.g., with restoration and crossing structures), especially for area-sensitive species during dispersal and mating movements. For these species occupancy is expected to be high in the core areas being connected, but not within the linkages themselves.

In summary, mapping and protecting linkages are critical to conserving wildlife, as is maintaining or increasing permeability to support landscape connectivity. Discounting the importance of linkage models is not warranted at this time and could hinder the development and implementation of landscape conservation plans. Further validation studies of connectivity models in general are needed, and we would like to see new programs and funding aimed at collecting data to further improve them. Validating connectivity models requires that researchers carefully consider model objectives, scale, and potential bias in data.

CRediT authorship contribution statement

A.T.H. Keeley: Writing – original draft, Writing – review & editing, Conceptualization. **P. Beier:** Writing – review & editing, Conceptualization. **R.T. Belote:** Writing – review & editing. **M. Clark:** Writing – review & editing, Conceptualization. **A.P. Clevenger:** Writing – review & editing, Conceptualization. **T.G. Creech:** Writing – review & editing, Conceptualization. **L. Ehlers:** Writing – review & editing, Conceptualization. **J. Faselt:** Writing – review & editing, Conceptualization. **M. Gogol-Prokurat:** Writing – review & editing, Writing – original draft, Conceptualization. **K.R. Hall:** Writing – review & editing, Conceptualization. **M.A. Hardy:** Writing – review & editing, Conceptualization. **J. A. Hilty:** Writing – review & editing. **A. Jones:** Writing – review & editing, Conceptualization. **T.A. Nuñez:** Writing – review & editing, Conceptualization. **K. Penrod:** Writing – review & editing, Conceptualization. **E.E. Poor:** Writing – review & editing, Conceptualization. **C. Schloss:** Writing – review & editing, Conceptualization. **D.M. Theobald:** Writing – review & editing, Conceptualization. **T. Smith:** Writing – review & editing, Conceptualization. **W.D. Spencer:** Writing – review & editing, Conceptualization. **R. Sutherland:** Writing – review & editing, Conceptualization. **G.M. Tabor:** Writing – review & editing, Conceptualization. **K.A. Zeller:** Writing – review & editing, Conceptualization.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

No data was used for the research described in the article.

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